

Pollination in Dioecious Figs

Pollination of *Ficus fistulosa* by *Ceratosolen hewitti*

By

J. GALIL

Department of Botany, Tel Aviv University, Israel

ABSTRACT

Pollination in the dioecious fig *Ficus fistulosa* was studied in Singapore. The pollinator, *Ceratosolen hewitti* (Agaonidae), possesses closed thoracic pockets and coxal combs. Pocket filling with pollen from detached anthers previously cut by the male wasps occurs in the almost ripe male figs. Pollen is lifted from the anther to the underside of the thorax by means of the arolia of the fore legs and then shoveled backwards into the pockets by the combs. In the male figs, pollination of the stigmata occurs at the end of oviposition prior to the withdrawal of the ovipositor. Pollen is taken directly from the pockets by the fore-legs and is carried downwards onto the stigmata. The behaviour of the female wasps in the female syconia is very similar except that the oviposition act does not culminate with actual egg-laying. The significance of pollination in short-styled, gall-producing flowers and of ovipositor insertion into the styles of long-styled, seed-producing flowers is discussed.

Introduction

It is known that the symbiotic wasps (Agaonidae, Chalcidoldea) which serve as pollen vectors in the genus *Ficus* carry out in the figs two types of activities namely, pollination of the long-styled flowers and oviposition into the pistils of the short-styled ones. Hence, the former produce seeds whereas the ovaries of the latter develop into galls and give rise to the next generation of wasps. Both activities are indispensable for the existence of fig symbiosis. There is no evidence of the presence of apomixis in *Ficus* so that pollination, too, appears to be essential for seed production. The question arises as to the occurrence of pollination in the short-styled flowers and oviposition into the long-styled ones.

In the common fig (*F. carica* L.), the most extensively studied *Ficus* sp. (Grandi, 1929), the situation is comparatively simple. Here, pollen is passively carried on the body of the female wasp *Blastophaga psenes* L. from one fig to another so that pollination of both long- and short-styled flowers takes place indiscriminately; on the other hand, the long styles, which so markedly differ in structure from the short styles, do not appear to be suitable for oviposition.

The situation is not always as simple in other *Ficus* spp. There is considerable variation in structure and behaviour of the pollinators of different species of *Ficus*, in spite of an overall resemblance. Unique organs used by various spp. of wasps as containers for transporting pollen from male figs (phase D*) to young receptive female figs (phase B*) were recently discovered (Ramirez, 1969; Galil and

* According to Galil and Eisikowitch (1968) the developmental phases of figs were named as follows:

Phase A (Pre-female): Young syconium prior to the opening of the ostiole.

Phase B (Female): Ostiolar scales loosen, female flowers ripen, sycophilous wasps penetrate into the syconium and oviposit into the ovaries.

Phase C (Interfloral): Wasp larvae and fig embryos develop within their respective ovaries. Ovaries occupied by the larvae are transformed into galls.

Phase D (Male): Male flowers mature, wasps reach the imago stage, fertilized female wasps leave syconia via channels bored by the males.

Phase E (Post-floral): Both syconia and the seeds inside them ripen.

Eisikowitch 1969; Galil and Snitzer-Pasternak, 1970; Galil et al., 1974). In these figs, the pollination process consists of "deliberate" loading of the containers and, upon entering the young figs, extracting the pollen and pollinating the female flowers. Actual pollination takes place at the end of the oviposition act, before the wasp withdraws her ovipositor from the pistil. Hitherto, pollination by wasps with specialized pollen containers was exclusively studied in monoecious figs that contain both long- and short-styled female flowers (the so-called seed- and gall-flowers, respectively) in the same syconium. Because of the dense packing of the flowers within such figs, it is very difficult to observe the behaviour of the wasps in regard to the different flower types. Nevertheless, there is some information available. Johri and Konar (1956) discovered fig embryos up to the octant stage in the short-styled ovaries of *F. religiosa* L. This is clear evidence of fertile pollination of the short styled flowers. "Seed figs" in which both long- and short-styled flowers bear normal seeds that are occasionally found in various species (Galil and Eisikowitch, 1971), provide further evidence of normal pollination in both types of flowers. On the other hand, the blackening of the upper part of the style in long-styled flowers of *F. religiosa*, observed by the same authors, indicates that the wasps insert their ovipositors into such pistils as well.

Direct observations of the behaviour of the wasps in long- and short-styled flowers in regard to pollination and oviposition were hitherto carried out only in the monoecious figs of *F. sycomorus* L. (Galil and Eisikowitch, 1976). However, since the two flower types in that species are very similar and cannot be distinguished from the above without destroying the fig, only a few sporadic observations could be made.

Dioecious fig species, in which long- and short-styled female flowers develop in different syconia, lend themselves more easily to detailed observations on wasp behaviour with regard to the two flower types. For such observation *Ficus* spp. whose pollinators are equipped with specialized pollen containers which are actively loaded and emptied must be chosen.

The dioecious figs of *F. fistulosa* Reinw. ex Bl. (Fig. 5) which belong to the *Sycocarpus* section of subgenus *Ficus* and are pollinated by *Ceratosolen hewitti* Waterston, possessing thoracic pockets for pollen transport, prove suitable for the present study.

Materials and Methods

The study was carried out in June-July, 1971 in Singapore. The chief object, *F. fistulosa*, is a small tree, 3 to 4 m. high, that grows abundantly along road edges in the suburbs of the town and on the borders of the jungle.

Generally, the study of pollination in dioecious figs is more complicated than in monoecious species since it is necessary to find wasp-releasing D-phase male figs and receptive B-phase figs of both sexes simultaneously in the same vicinity. The month of June proved to be very suitable since it is a period of overlapping of the two main crops of figs in *F. fistulosa*. Hence, all of the required developmental phases of the figs were available (for Hong Kong, see also Hill, 1967). During the study, no ripening female figs were found, but these were not indispensable for carrying out the necessary observations.

The cauliflorous figs of *F. fistulosa* develop in great numbers, provide abundant and easily accessible material. The timing of observations was adjusted to the activities of the wasps in the male and female phases of the fig. Hence, the

observations on pocket filling were carried out in the early morning, between 3 and 5 a.m.

For observing the behaviour of the wasps in young figs during oviposition and pollination, B-phase figs, male and female separately, were enclosed in plastic vials covered with insect-proof netting together with wasp-releasing D-phase male figs. The emerging wasps which penetrated the receptive B-phase figs provided good material for observation of wasp behaviour during oviposition and pollination.

Observations

Syconia and pollinators

The figs develop on small lateral shoots on the trunks and branches (Fig. 6). The receptive (phase B) figs of both sexes are pear-shaped with a short neck and are borne on distinct peduncles that are up to 25 mm long (Fig. 7). The male figs are somewhat larger than female figs, 14 x 16 mm as compared to 11 x 13 mm. The ostiole is depressed and is sealed by imbricate scales. The structural features of the fig are especially prominent when bisected figs are viewed from the inner side (Figs. 8, 9). The different components have different colours: the ostiolar scales are orange and the pale stigmata stand out on the background of crimson ovaries. The internal cavity of the fig is wide and distinct.

The male figs contain a large number of short-styled female flowers ("gall flowers") covering almost the entire inner surface of the fig and 30 to 35 ostiolar male flowers arranged in one to two rows (Fig. 8). The male flowers are relatively prominent and easily discernable, but are still closed and unripe. The "gall flowers" are almost hidden within the fused perianth lobes (Fig. 1, II). The short (about 0.3 mm) and relatively thick style and the funnel-shaped stigma at its end project out of the perianth. The broad and dense stigmata form a continuous surface around the fig cavity but do not coalesce into a single "synstigma".

The long-styled female flowers ("seed flowers") which cover the entire inner surface of the female figs are quite different from the short-styled ones. The perianth is much reduced thus forming a narrow ring at the base of the ovary (Fig. 1, III). Consequently, the pistils are naked and visible for their entire length in bisected figs. The ovary is smaller and the style is narrower and much longer (about 1 mm) than their counterparts in the short-styled flowers. The stigma is cylindrical, thick and long (0.16 x 0.3 mm).

At the wasp-releasing stage (phase D), the male figs are almost globose (Fig. 10), somewhat broader than high (20 x 25 mm). The holes in the empty gall-ovaries from which the wasps have already emerged have rounded lids which are shifted to the side (Fig. 12).

Upon ripening of the male flowers, the filament of the single stamen elongates so that the anther is pushed through the top of the fused perianth (Fig. 1, I). At this stage, the males of the pollinating wasps approach the male flowers and cut off some of the anthers causing them to be scattered within the cavity of the fig. Thus, the emerging female wasps encounter cut anthers in addition to the intact stamens remaining *in situ* around the ostiole (Fig. 11). At the end of phase D, a large hole is cut through the scales in the centre of the ostiole by the male wasps (Fig. 12). The pollen loaded females emerge from the fig through this hole.

After the liberation of the wasps, the fig grows rapidly, and at ripening (Phase E) it reaches about 30 mm in diameter. It becomes yellowish and attains a characteristic smell which is typical for bat-dispersed fruit.

As noted above, no ripe female figs of *F. fistulosa* were found throughout the period of the present study. Hill (1967) states that the ripe female figs are somewhat smaller than the male figs, but are more succulent and their yellow colour is more pronounced.

The pollinator, *Ceratosolen hewitti* Waterston (Wiebes, 1963, 1966; Grandi, 1963) is a small agaonid wasp about 1.5 mm long (Fig. 2). Only those characteristics of the female wasp that pertain to pollination will be described below.

Of the two types of specific pollen containers hitherto described in pollinators of *Ficus*, namely "coxal corbiculae" and "thoracic pockets" (Ramirez, 1969; Galil et al., 1974), the female of *C. hewitti* possesses the latter only. In whole mounts of the ventrum of the body, the pockets appear on both sides of the mesothorax as triangular depressions that are entirely covered by continuous flaps (Fig. 3). Generally, the structure of the pockets is quite similar to that of the corresponding organs described in *C. arabicus* Mayr, the pollinator of *F. sycomorus* L. in East Africa (Galil and Eisikowitch, 1969). It appears that the pockets open and close along their inner suture facing the median axis of the body through changing in the position of the covering flaps.

Coxal corbiculae such as described by Ramirez (1969) and Galil et al. (1974) were not found on the fore coxae of *C. hewitti*. There are no depressions along the coxae; only the comb, namely the row of stiff bristles which usually fringe the depression on its inner side, is found here. In *C. hewitti*, the comb is a distinct organ formed from a straight row of about 18.38μ -long bristles (Fig. 4).

The length of the ovipositor of the pollinating wasp is of decisive importance in fig symbiosis. As seen from the side, the ovipositor of *C. hewitti* scarcely projects beyond the apex of the body. In fact, the ovipositor is not short but arises at some distance forwards, on the under side of the abdomen. Its real length may be seen during egg-laying when its shaft is released from the protecting valves and is directed towards the stigmata.

Pocket loading

Detailed observations of the filling of pockets of *C. hewitti* in D-phase male figs of *F. fistulosa* are not easy. Figs with ostiolar male flowers are usually suitable for such observations. However, in *F. fistulosa* the situation becomes more complicated because of the early emergence of the female wasps from their galls and the filling of the pockets prior to the tunnelling of the syconial wall by the male-wasps. For successful observation of pocket loading, the figs must be cut and studied during a comparatively short lapse of time when the anthers are still attached but sufficiently ripe, and the fertilized females have not yet left their galls.

When the figs are cut at the appropriate time, the female wasps become active, emerge from the galls, approach the male flowers and start filling their pockets from the anthers which protrude out of the floral perianth.

Lifting of the pollen from the anthers to the side of the thorax is accomplished by rapid alternating movements of the forelegs. Similar movements were observed in the pollinators of monoecious figs previously studied. Clumps of pollen are

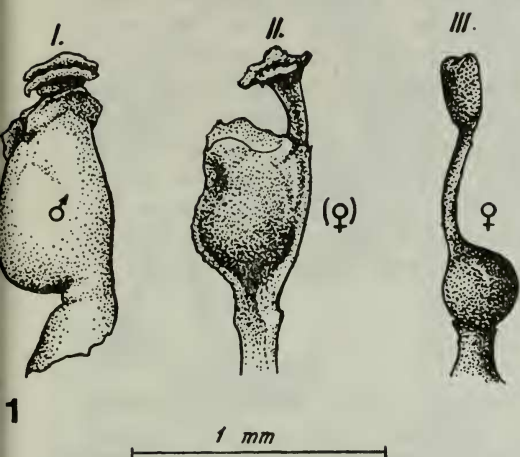
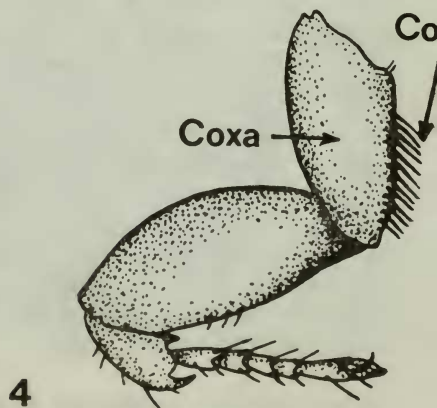
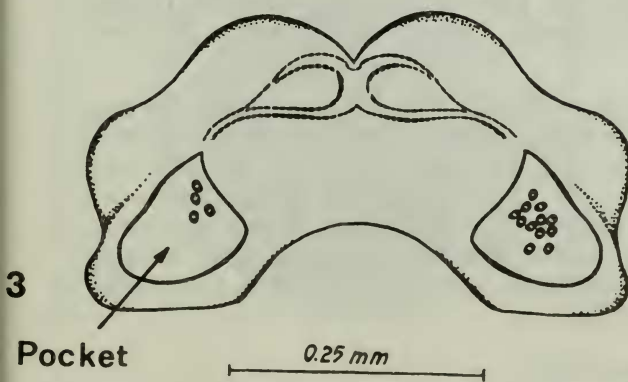
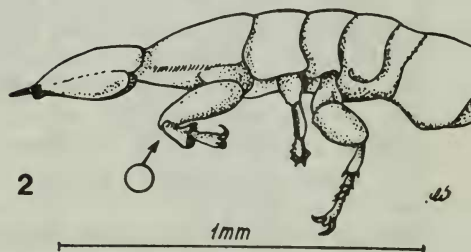
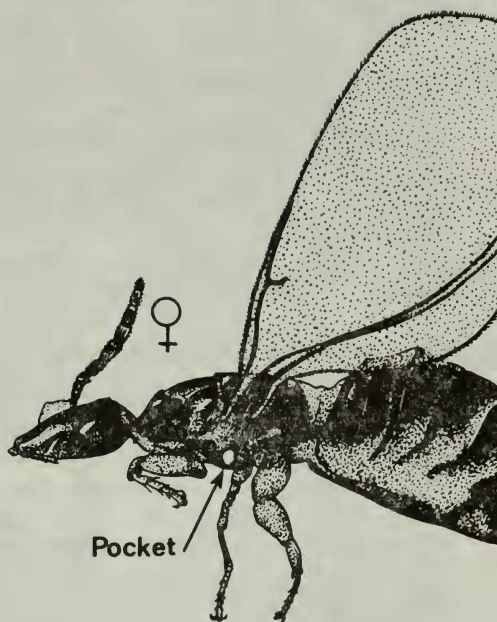


Fig. 1. *Ficus fistulosa*, flowers: I—male flower; II—short-styled female flower (♀); III—long-styled female flower ♀.

Fig. 2. *Ceratosolen hewitti* (♀ and ♂).

Fig. 3. Mesothorax of *Ceratosolen hewitti* (from below) showing pollen pockets.

Fig. 4. Fore leg of *Ceratosolen hewitti*, with comb.



placed between the body wall and the fore coxae which move up and down when the pollen is lifted by the bending legs. Shovelling movements of the fore coxae and combs by which the pollen is brushed backwards from the underside of the thorax to the thoracic pockets occur after each sequence of pollen liftings. The coxal comb is clearly a unique organ and even in the absence of the coxal depression ("corbicula"), it has a particular role in pocket filling. The shovelling movements are rapid but can be clearly seen. The role of the combs in the brushing of the pollen is evident from the pollen grains which are found on the bristles. When the quantity of pollen in the anther does not suffice for the filling of the pockets, the wasp moves to a second anther and begins a new series of liftings and shovelling movements.

Pocket emptying: pollination in male figs

The observations on the behaviour of the female wasps during oviposition and pollination were especially successful in the early morning when B-phase receptive figs were enclosed in plastic vials together with wasp-releasing D-phase male figs. As in the monoecious *Ficus* spp. previously studied (Galil and Eisikowitch, 1969; Galil et al., 1974), the impregnated and pollen-carrying female wasp starts to oviposit and to pollinate the stigmata immediately after its entrance into the receptive fig. In *C. hewitti*, as usual in the agaonid wasps, the ovipositor shaft is released from the protecting valves at the beginning of oviposition act and is supported and guided to the stigmata by the sternites that fold lengthwise to form a triangular, gutter-shaped, body. The total length of the ovipositor is about 0.8 mm., i.e. its length is intermediate between that of the styles in long- and short-styled flowers. After several probing movements for an appropriate oviposition site, the ovipositor sinks into one of the funnel-shaped stigmata of the short-styled flowers. It remains in the style only for 15 to 18 seconds which is a very short time compared to the duration of the act in pollinators of other figs previously studied, i.e. about 60 seconds in *C. arabicus*, and 3 to 3.5 minutes in *Blastophaga estherae* Grnd., the pollinator of *F. costaricana* (Liebm.) Miq. (Galil et al., 1974). Almost immediately after the insertion of the ovipositor into the pistil of the flower, the female wasp begins to perform typical pollination movements. The forelegs fold upwards upon themselves one after the other intermittantly, thereby bringing the arolia into contact with the pollen pockets on the under side of the mesothorax.

The pollen grains are taken up by the legs directly from the pockets; in any case, no shovelling of pollen from the pockets by means of the combs of the fore coxae were observed. The pollen-carrying legs open downwards one after the other and touch the stigmata beneath. It is apparent that normal pollination of the short-styled flowers takes place systematically at the end of each oviposition act. During oviposition and pollination, the head of the female wasp remains motionless and no biting of the stigmata takes place, as observed in *C. arabicus* (Galil and Eisikowitch, 1969).

Pocket emptying: pollination in female figs

In spite of the distinct differences in the structure of the pistils in the female flowers of the male and female figs, the behaviour of the wasps was almost alike. As in the male figs, the female wasps moved on the surface of the stigmata, inserted the ovipositors into them one by one and performed the characteristic pollination movements at the end of each insertion. The retention of the ovipositor

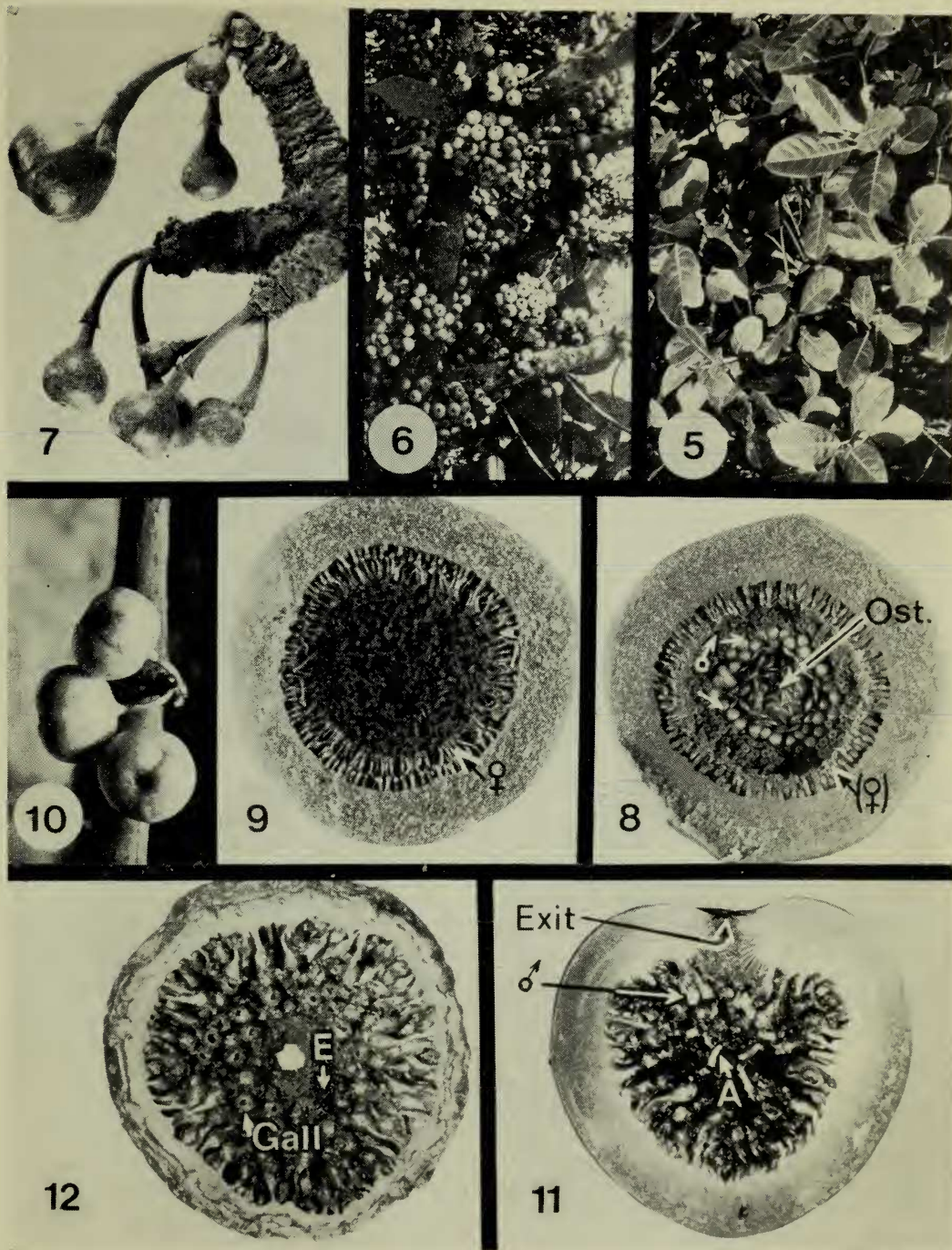


Plate 1.

Figs. 5-12 *Ficus fistulosa*

Fig. 5. Leafy branches. Fig. 6. Fruiting stem. Fig. 7. Short branch with male figs at Phase B. x 0.7. Fig. 8. Cross section through male fig at phase B. (♀) — short-styled female flowers. ♂ — unripe male flowers. x 3.7. Fig. 9. Cross section through female fig at phase D. ♀ — long-styled female flowers. Fig. 10. Male figs at phase D. x 0.6. Fig. 11. Longitudinal section through male fig after release of wasps. ♂ — attached anthers; A — detached anthers; x 2.3. Fig. 12. Cross section through male fig at phase D showing bare area E around ostiole. x 2.2.

within the style was shorter than in the short-styled flowers and lasted barely 8 to 10 seconds. Here also pollen is transferred directly from the thoracic pockets onto the stigmata of the long-styled female flowers by the arolia of the fore legs.

During these observations, several cases of unusual behaviour of the wasps in the female figs were encountered. Exhausted female wasps, which have already completed their usual activities, continued to move their fore legs in vain efforts to extract pollen from the pockets and to deposit it on the stigmata.

In order to observe this phenomenon more closely, pollen loaded female wasps were taped in a supine position on a glass slide and observed through the dissecting microscope immediately after they emerged from the D-phase male figs. Most of the wasps made vain attempts to get off the glass; however, in a few cases, the wasps started to perform the characteristic pollination movements during which they folded the fore legs onto the thorax and inserted the arolia into the widely gaping pollen pockets. Pollen grains could be clearly seen on the arolia. No such movements have hitherto been seen in the pollinators of the monoecious figs in which pollination has been studied.

Discussion

In spite of numerous structural differences between the syconia of dioecious *F. fistulosa* and monoecious *F. sycomorus* (Galil and Eisikowitch, 1969) which belong to different subgenera of *Ficus*, namely subgenus *Ficus* and subgenus *Sycomorus* respectively, the two have several biological features in common. Of particular significance is the relatively small number of male flowers which reflects the efficiency of the pollen vectors in pollen transfer. In both *Ficus* taxa, the pollinating wasps are species of *Ceratosolen* possessing closed thoracic pollen pockets of similar structure and coxal combs without corbiculae, and behave very similarly in relation to the figs. In both species, the male wasps cut the stamens and the females emerge from their galls, fill their pockets with pollen from the detached anthers and gather in the fig cavity before the syconial wall is tunnelled by the males. Also the behaviour of the female wasps during pocket filling and emptying, i.e. pollination, is similar. Such likenesses indicate that physiological conditions within the figs are probably also similar in both cases (Galil et al., 1973).

In *F. fistulosa*, the behaviour of the female wasps in the short- and long-styled female flowers (in different figs!) is almost identical in spite of the structural differences between them. In the two types of flowers, both insertion of the ovipositor into the style and deposition of pollen on the stigmas take place. Essentially, it is the same process although eggs are not likely to be laid within the long-styled pistils. In *F. sycomorus*, serial microtome sections through long-styled pistils in pollinated figs failed to reveal any remnants of *Ceratosolen* ova. The pistils of the long-styled flowers of *F. fistulosa* have not been similarly investigated but there are some indirect indications that here too, no real oviposition takes place. The relatively much shorter time that the ovipositor remains in the long styles is significant. It appears that for effective oviposition, the stimulus which the flower ovary exerts on the tip of the ovipositor is indispensable. Consequently, when the style is too long and the ovary is beyond the reach of the ovipositor, there is no egg-laying.